

Comparison of the Chapman-Richards Function with the Schnute Model in Stand growth

Li Fengri (李凤日)

Northeast Forestry University, Harbin 150040, P. R. China

Wang Yonghe (王永和)

Canadian Forest Service, Ontario P6A 5M7, Canada

Hou Lijun (侯丽君)

Xinlin Forest Bureau, Daxing'an Mountain District, Heilongjiang Province

Abstract: The Chapman-Richards Function and its two exception cases in applications were discussed and compared with the Schnute model in stand growth studies. Compared from all perspective, it was found that the Schnute model commonly used in forestry was identical to the Chapman-Richards function. If some parameter in the Chapman-Richards Function was unconstraint, the function could also be very versatile to fit some exceptional growth curves, the fitted function should be identical to that the Schnute model.

Key words: Chapman-Richards Function, Schnute model, Stand growth, Model fitting

Introduction

As a growth model for an individual tree or forest stand, the Chapman-Richards Function, an extension to the Von Bertalanffy's growth theory (Bertalanffy 1957) embodies all other established growth function. This function has been widely used in forestry because of its flexibility, accuracy, and meaningful analytical properties (Cooper 1996, Pienaar and Turnbull 1973, Osumi and Ishikawa 1983, Ito and Osumi 1984).

Based on a simple biological theory of accelerating growth, Schnute (1981) developed a new and comprehensive growth model with statistically stable parameter, that was said to cover all other growth functions existing to date. The Schnute model seems to have been accepted quickly because of its versatility and stable parameter estimation (Bredenkamp and Gregoire 1988, Yang and Feng 1989, Zeide 1993). Bredenkamp and Gregoire (1988) and Yang and Feng (1989) studied the performance of the Chapman-Richards Function along with the Schnute model. They concluded that the competition mortality, the stand resumed growth beyond what appeared to be an asymptotic level where the Chapman-Richards Function did not fit the data satisfactorily. Meanwhile, the Schnute model can tract such a trend in growth successfully.

The above conclusion was drawn probably because the model was only used for data fitting, biological and local asymptotic properties of parameters might have been neglected. In this paper we demonstrate that the

Chapman-Richards function and the Schnute model have the same capability, they can fit the same data set equally well and with the same accuracy. The objective of this study is to compare the two models to show the relation between them.

The Chapman-Richards Function

In studying plant growth, Richards (1959) proposed to extend the range of parameter m in Von Bertalanffy's growth model to $m > 0$ rather than $m > 1$, i.e.,

$$\frac{dy}{dt} = \eta y^m - \kappa y \quad (1)$$

Where y is a measure of plant volume, t is plant age, η , κ and m are parameters. It is also assumed that η and $\kappa < 0$ if $m > 1$, η and $\kappa > 0$ if $0 < m < 1$. By integrating equation (1) with the initial condition of $y=y_0$ for $t=0$, the Chapman-Richards function is obtained as

$$y = A(1 - Be^{-Kt})^{\frac{1}{1-m}}, \quad 0 < m < 1 \quad (2)$$
$$y = A(1 + Be^{-Kt})^{\frac{1}{1-m}}, \quad m > 1$$

with

$$A = \left(\frac{\eta}{\kappa}\right)^{\frac{1}{1-m}}, \quad B = \frac{\frac{\eta}{\kappa} - y_0^{\frac{1}{1-m}}}{\eta}, \quad K = (1-m)\kappa$$

where A is the asymptote, m determines the shape and inflection point of the growth function, and K is related

to growth rate. Equation (2) has the following properties:

- It has asymptote A , $y \rightarrow A$ as $t \rightarrow \infty$.
- y is a monatomic increasing function of t .
- The inflection point is at:

$$t_f = \frac{1}{K} \ln\left(\frac{B}{1-m}\right), y_f = A m^{1/m} \text{ when } 0 < m < 1 \quad (3)$$

$$t_f = \frac{1}{K} \ln\left(\frac{b}{1-m}\right), y_f = A m^{1/m} \text{ when } m > 1$$

- The curve has a cross-over point at:

$$t_0 = \frac{1}{K} \ln(B) \quad (4)$$

such that $y=0$ at $t=t_0$.

In addition to $m > 0$, the following two exceptions could occur in actual applications.

Case 1

For $\kappa < 0$ and $\eta, \kappa' > 0$, equation (2) was fitted to some DBH data of fast-growing species with no inflection point. The trees continue growing from an early age as shown in Figure 1 and the corresponding growth function should be:

$$y = A(1 - Be^{-Kt})^{1/m}, \text{ with } A, B, K > 0, m < 0 \quad (5)$$

Equation (5) does not have an inflection point because $m < 0$ (see y_f in equation (3)).

Case 2:

For $m < 0$, $\eta > 0$, and $\kappa < 0$, let $\kappa' = -\kappa$, then (1) become

$$\frac{dy}{dt} = \eta y^m + \kappa' y, \eta, \kappa' > 0, m < 0 \quad (6)$$

The solution to (6) with initial condition is:

$$y = A'(Be^{-Kt} - 1)^{1/m}, A', B', C' > 0, m < 0 \quad (7)$$

where

$$A' = \left(\frac{1}{\kappa'}\right)^{1/m}, B' = 1 + \left(\frac{y_0}{A'}\right)^{1/m}, K' = \kappa'(1-m)$$

Equation does not have an asymptote. After the curve passes the point (t_1, y_1) , dy/dt begins to increase as t increase. Such a growth curve is analogous to the one shown in Figure 2. The inflection and cross-over points for (7) are:

$$t_f = \left(\frac{1}{K'}\right) \ln\left(\frac{1-m}{B'}\right), y_f = A'(1-m)^{1/m} \quad (8)$$

$$t_0 = \frac{1}{K} \ln\left(\frac{1}{B}\right) \quad (9)$$

Equation (7), a species case of the Chapman-Richards function, can describe the growth pattern of a stand resuming growth beyond what had appeared to be an asymptotic level after marked competition mortality (Bredenkam and Gregoire 1988).

The Schnute Growth Model

The Schnute model used in forestry is developed as follow: Let $Y(t)$ be the size of an organism with growth rate dY/dt and relative growth rate $Z = \frac{1}{Y} \frac{dY}{dt}$. The relative growth rate of Z , $\frac{dZ}{dt}$, is assumed to be a linear function of Z as:

$$\frac{1}{Z} \frac{dZ}{dt} = -(a + bZ) \quad (10)$$

where $a \neq 0$ and $b \neq 0$ are parameters. Since $a \neq 0$ and $b \neq 0$, the growth could be accelerating or both. (10) has another form:

$$\left(\frac{b}{a+bZ} - \frac{1}{Z}\right) dZ = a dt \quad (11)$$

Integrating (11) with the initial condition of $t = T_1$ and $Z(T_1) = Z_1$ is an unknown constant gives:

$$\ln\left(\frac{a+bZ}{Z} - \frac{Z_1}{a+bZ_1}\right) = a(t - T_1) \quad (12)$$

From (12) $Z(t)$ can be written as:

$$\begin{aligned} \frac{d \ln(Y)}{dt} = Z(t) &= \frac{aZ_1 e^{-a(t-T_1)}}{a+bZ_1(1-e^{-a(t-T_1)})} \\ &= \frac{1}{b} \frac{d}{dt} \ln(a+bZ_1(1-e^{-a(t-T_1)})) \end{aligned} \quad (13)$$

The solution to (13) with $y=y_1$ at $t=T_1$ is:

$$Y(t) = y_1 \left(\frac{a+bZ_1(1-e^{-a(t-T_1)})}{a} \right)^{1/b} \quad (14)$$

where integration contant Z_1 can be solved using the terminal condition of $t = T_2$ and $Y(t) = y_2$ as:

$$Z_1 = \frac{a(y_2^{1/b} - y_1^{1/b})}{b(y_1^{1/b} (1 - e^{-a(T_2 - T_1)}))} \quad (15)$$

Substituting Z_1 into (14) gives the explicit solutions to (10) or the Schnute model as

$$Y(t) = (y_1^h + (y_2^h - y_1^h) \frac{1 - e^{-a(t-T_1)}}{1 - e^{-a(T_2-T_1)}})^h \quad (16)$$

where T_1 and T_2 are initial and terminal ages, y_1 and y_2 are corresponding size at T_1 and T_2 .

By definition, t_0 is the value of t such that $Y(t)=0$. Let (16) equal to 0, t_0 is derived as:

$$t_0 = T_1 + T_2 - \frac{1}{a} \ln \left(\frac{e^{aT_2} y_2^h - e^{aT_1} y_1^h}{y_2^h - y_1^h} \right) \quad (17)$$

(16) has the upper asymptote as:

$$y_\infty = \left(\frac{e^{aT_2} y_2^h - e^{aT_1} y_1^h}{e^{aT_2} - e^{aT_1}} \right)^h \quad (18)$$

The inflection point is at:

$$t^* = T_1 + T_2 - \frac{1}{a} \ln \left(\frac{b(e^{aT_2} y_2^h - e^{aT_1} y_1^h)}{y_2^h - y_1^h} \right), \quad (19)$$

$$y^* = \left(\frac{(1-b)(e^{aT_2} y_2^h - e^{aT_1} y_1^h)}{e^{aT_2} - e^{aT_1}} \right)^h$$

Relationships between the Two Models

By comparing assumptions, solutions and relations among the parameters for the two models, one can show that they are interchangeable.

Identical differential equations

If η , κ , and m in equation (1) are unconstrained or:

$$\frac{dy}{dt} = \eta y^m - \kappa y, \quad \eta, \kappa, m \text{ are any constant} \quad (20)$$

multiplying both sides of (20) by y^{-1} gives:

$$Z(t) = \frac{1}{y} \frac{dy}{dt} = \eta y^{m-1} - \kappa \quad (21)$$

Differentiating (21) by dt gives:

$$\frac{dZ}{dt} = \eta(m-1)y^{m-2} \frac{dy}{dt} = (m-1)\eta y^{m-1}Z \quad (22)$$

Equation (21) indicates that $\eta y^{m-1} = Z + \kappa$, substituting this into (22) gives:

$$\frac{1}{Z} \frac{dZ}{dt} = -(\kappa(1-m) + (1-m)Z) \quad (23)$$

Let $a=\kappa(1-m)$ and $b=1-m$, then (23) becomes (10) or the differential equation for the Schnute model. The Schnute model can be derived from the assumption for the Chapman-Richards function and vice-versa. From (B2) and (B5) (see Appendix B), there exist:

$$Z = c_1 e^{-\eta t} (a + bZ) \quad (24)$$

and

$$y = c_2 (1 - c_1 b e^{-\eta t})^{\frac{1}{b}} \quad (25)$$

where c_1 and c_2 are integration constants. From equation (24) we can get $c_1 e^{-\eta t} Z / (a + bZ)$, substituting this into (25) generates:

$$y^h = c_2^h \frac{a}{a + bZ} \quad (26)$$

Since $Z=(1/y)(dy/dt)$, (26) can be written as:

$$\frac{dy}{dt} = \frac{a}{b} c_2^h y^{1/h} - \frac{a}{b} y \quad (27)$$

Let $m=1-b$, $\kappa=a/b$, $\eta=(a/b)c_2^h$ then (27) becomes (20), which is the differential equation for the Chapman-Richards function. The above exercise proves that the two model have same differential equation with unconstrained parameters.

Identical solution set for the general solutions

It is shown in Appendices A and B that the general solutions to the two differential equations have the same formulation, their parameters are interchangeable. For example, the parameters in the general solution for the Chapman-Richards function (A5) can be written as:

$$m = 1 - b, \quad \kappa = \frac{a}{b}, \quad \eta = \left(\frac{a}{b} \right) c_2^h, \quad c_3 = a c_1 c_2^h$$

where a , b , c_1 , and c_2 are parameters in the solution for the Schnute model (B5). Similarly, a , b , c_1 and c_2 can be expressed as:

$$a = \kappa(1-m), \quad b = 1-m, \quad c_2 = \left(\frac{\eta}{\kappa} \right)^{\frac{1}{1-m}}, \quad c_1 = \frac{c_3}{\eta(1-m)}$$

Identical explicit solution

The general solution to (20) is:

$$y = \left(\frac{\eta}{\kappa} + c e^{\kappa(1-m)t} \right)^{\frac{1}{1-m}} \quad (28)$$

where c is the integration constant. With the initial condition of $t = T_1$ and $Y(t) = y_1$, c becomes:

$$c = \left(y_1^{\frac{1}{1-m}} - \frac{\eta}{\kappa} \right) e^{\kappa(1-m)T_1} \quad (29)$$

Putting c back into (28) to have:

$$Y(t) = \left(\frac{\eta}{\kappa} + \left(y_1^{1-m} - \frac{\eta}{\kappa} \right) e^{-\kappa(1-m)(t-T_1)} \right)^{\frac{1}{1-m}} \quad (30)$$

η/κ can be solved with the terminal condition of $t = T_2$ and $Y(t) = y_2$. Substitute η/κ into (30) and use $b = (1-m)$, $a = \kappa(1-m)$, then the solution to (20) is:

$$Y(t) = (y_1^b + (y_2^b - y_1^b) \frac{1 - e^{-a(t-T_1)}}{1 - e^{-a(T_2-T_1)}})^b \quad (31)$$

which is the Schnute growth model.

The above analysis reveals that if the parameters in Von Bertalanffy's model are not constrained and the two stages are given for a growth process, then the Schnute model can be deduced from (20) by using the initial condition of (T_1, Y_1) to get a specific solution first, then the terminal condition of (T_2, y_2) is used to replace η/κ (in equation (30)) which is related to the asymptotic parameter $A(\eta/\kappa = A^{1-m})$ in Chapman-Richards function. In this case, the Schnute model is an explicit solution to (20) with an implicit asymptotic parameter.

The relation between two sets of parameters

Parameters a and b in the Schnute model can be represented by those in the Chapman-Richards function as:

$$a = K = (1-m)\kappa$$

$$b = 1-m \text{ (or } m = 1-b\text{)}$$

Similarly, there are:

$$A = \left(\pm \left(y_1^b + \frac{y_2^b - y_1^b}{1 - e^{-a(T_2-T_1)}} \right)^{\frac{1}{b}} \right)$$

$$B = \pm \frac{e^{a(T_2-T_1)}(y_2^b - y_1^b)}{e^{aT_2}y_2^b - e^{aT_1}y_1^b}$$

such that $A > 0$ and $B > 0$

Whether the two model have the asymptote or not is

Table 1. The parameters estimated for equation (2) and (16)

Density	The Chapman-Richards function									
	A	B	K	m	RSS	DF	MSE	t_0	t_1	y_1
3.1 × 3.1	567.5702	0.8291	0.1510	0.8907	918.643	23	39.9410	-1.2413	13.4197	197
2.3 × 2.3	644.397	1.4379	0.1465	0.7362	8077.233	23	351.1841	2.4791	11.5750	202
1.9 × 1.9	804.9043	1.5185	0.1146	0.6328	1079.113	23	46.9180	3.6301	12.3726	231
1.7 × 1.7	796.7438	1.5093	0.0865	0.4820	11341.77	23	493.1205	4.7608	10.8283	175
1.5 × 1.5	1285.9725	1.2163	0.0395	0.0827	10650.108	23	463.0482	4.9590	7.1457	85

Density	The Schnute model										
	y_s	y_1	y_2	a	b	RSS	DF	MSE	t_0	t^*	y^*
3.1 × 3.1	567.5702	6.1977	498.57	0.1510	0.1094	918.643	23	39.9410	-1.2413	13.4197	197
2.3 × 2.3	644.369	7.4926	579.65	0.1465	0.2383	8077.233	23	351.1841	2.4791	11.5750	202
1.9 × 1.9	804.9043	4.2045	622.26	0.1146	0.3672	1079.113	23	46.9180	3.6301	12.3726	231
1.7 × 1.7	796.7438	1.1152	609.99	0.0865	9.5918	11341.77	23	493.1205	4.7608	10.8283	175
1.5 × 1.5	1285.9725	1.1668	711.66	0.0395	0.9173	10650.11	23	463.0482	4.9590	7.1457	85

Note: (1) $T_1=7$ and $T_2=27$, (2) t is stand age(year) and y is stand volume (m^3)

decided by m and κ or a and b . The asymptote exist if $0 < m < 1$ ($0 < b < 1$) and $\kappa > 0$ ($a > 0$) or $m < 0$ ($b > 1$) and $\kappa > 0$ ($a > 0$). If $m > 1$, the asymptote exists only if

$$a > \frac{-b \ln(\frac{y_2}{y_1})}{T_2 - T_1}$$

The relation between the cross-over and inflection points

The cross-over point of the Schnute model can be derived from that of the Chapman-Richards function:

$$t_0 = \frac{1}{K} \ln(B) = \frac{1}{a} \ln\left(\frac{e^{a(T_1+T_2)}(y_2^b - y_1^b)}{e^{aT_2}y_2^b - e^{aT_1}y_1^b}\right)$$

$$= T_1 + T_2 - \frac{1}{a} \ln\left(\frac{e^{aT_2}y_2^b - e^{aT_1}y_1^b}{y_2^b - y_1^b}\right)$$

In the same fashion, (19) can be transformed from (3), implying points (t_1, y_1) and (t^*, y^*) are identical. The relation between asymptotes A and y_{∞} is obvious.

Examples

Two examples are used to verify the above results.

Example 1

Yang and Feng (1989) used both model to study the volume growth of permanent sample plots of *Cryptomeria* spp with 5 initial densities. Table 1 consists of the parameters by Yang and Feng (1989). With the given relations between the parameter, parameters A , B , κ , and m in the Chapman-Richards function could also be calculated from the value of y_1 , y_2 , a , and b in the Schnute model. The calculated results are the same as the fitted ones. Since $0 < m < 1$ (or $0 < b < 1$), the inflection point, asymptote, and t_0 exist for all 5 initial densities.

Example 2.

Bredenkamp and Gregoire(1988) fitted both models to the mean diameter growth data of *Eucalyptus grandis* plantations with 12 initial densities. Table 2 contains the estimated parameters and mean squared residuals

(MSE) from both models (Bredenkamp and Gregoire 1988) with some re-arrangement. Missing values in the table indicates the case where the Chapman-Richards function failed.

Table 2 Estimated coefficients from both-parameter Chapman-Richards and Schnute models to describe the dbh development of *Eucalyptus grandis* stand(Missing values indicate stand densities where the Chapman-Richards model could not be adequately fitted (Bredenkamp and Grgoire 1989).

Density	Chapman-Richards					Schnute				
	A	B	K	m	MSE	y_1	y_2	a	b	MSE
25	950.56	1.0632	0.0938	0.1948	2354.61	38.90	893.18	0.0938	0.8052	2354.61
62	838.15	1.0989	0.0883	0.0204	208.78	29.29	786.38	0.0883	0.9796	208.78
124	712.09	1.1168	0.1030	-0.0074	189.90	31.43	685.26	0.1030	1.0074	189.90
247	559.43	1.1365	0.0973	-0.3207	133.09	26.51	539.57	0.0973	1.3206	133.09
371	489.55	1.1302	0.0877	-0.5913	218.17	25.66	469.80	0.0877	1.5916	218.17
494	420.03	1.1439	0.0955	-0.7161	90.39	26.53	407.72	0.0955	1.7161	90.39
741	370.84	1.1543	0.1014	-0.8047	106.10	26.52	362.26	0.1014	1.8046	106.10
988	338.65	1.1129	0.0741	-1.1164	168.72	25.41	322.57	0.0741	2.1159	168.72
1482	326.95	1.0556	0.0368	-1.7056	96.05	27.25	284.30	0.0368	2.7056	96.05
2965						32.96	272.73	-0.0247	3.4050	99.64
4304						30.49	258.63	-0.0590	3.6780	71.75
6726						29.90	284.24	-0.1076	4.1654	71.76

Note: Bredenkamp and Gregoire (1989) used c_0 , c_1 , c_2 , and c_3 as the parameters for the Chapman-Richards function, in Table 2, $A=c_0$, $K=c_1$, $m=1-1/c_2$ and $B=c_3$. The DBH was measured in mm

The estimated parameters for the two model match and the MSE's are the same for the fist 9 densities. There are inflection point, asymptote, and t_0 for the first two densities since $0 < m < 1$ ($0 < b < 1$). As for densities 3 to 9 (124-1482 stems /hm²), only asymptote and t_0 exist because $m < 0$ ($b < 1$), which is the first exception for the Chapman-Richards function or (5) (see Fig. 1).

fitted(Bredenkamp and Gregoire 1988). This situation is graphically portrayed by Fig. 2. For the Schnute model, there are $b > 1$ and $A < 0$. It seems the asymptote and inflection point do not exist, only t_0 could be found. As point out by Schnute(1981), his model may not have inflection point for $b > 1$, however, the inflection point does exist if:

$$\frac{-b \ln(\frac{y_2}{y_1})}{T_2 - T_1} < a \leq 0$$

Parameter a for the last three densities was tested to satisfy the above condition. For example, the value of a for the density of 6726 stems/hm² is

$$\frac{-4.165 \ln(\frac{284.24}{29.90})}{32.83 - 1.50} = -0.2994 < a = -0.1076 < 0$$

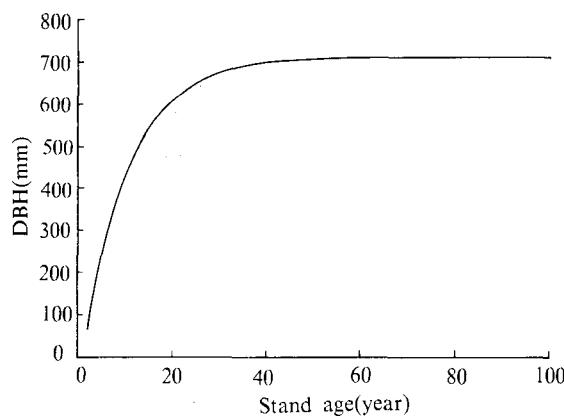


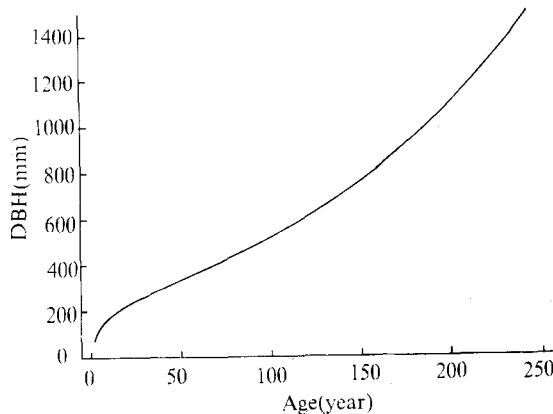
Fig. 1. The growth curve predicted by equation (5).

The parameters used are those for the density of 124 stems/hm² in Table 2

The Chapman-Richards function could not fit the data for the last three densities (2965-6726 stems/ hm²) because after competition mortality, the stand resumed growth and the model could no longer be satisfactorily

with $T_1 = 1.50$ and $T_2 = 32.83$ (Bredenkamp and Gregoire 1988). Therefor, not only the curve $t_0=1.48$, it also has the inflection point at:

$$t^* = T_1 + T_2 - \frac{1}{a} \ln(\frac{e^{aT_2} y_2^b - e^{aT_1} y_1^b}{y_2^b - y_1^b}) = 14.74$$

**Fig. 2 The growth curve predicted by (7).**

The parameters used are those for the density of 2965 stems/hm² in Table 3

It is determined that the following is common for the last three densities, i.e., for the Schnute model, there are $a < 0$ and $b > 1$, for the Chapman-Richards function, $m < 0$

Table 3. The value parameter A , B , κ , and m calculated from y_1 , y_2 , a and b for the last three densities

density	Chapman-Richards				Schnute				MSE
	A	B	κ	m	y_1	y_2	a	b	
2965	260.439	0.9645	-0.0247	-2.4050	32.96	272.73	-0.0247	3.4050	99.64
4304	163.8167	0.9172	-0.0590	-2.6780	30.49	258.63	-0.0590	3.6780	71.75
6726	127.5245	0.8530	-0.1076	-3.1654	29.90	284.24	-0.1076	4.1654	71.76

Table 4. the predicted value for the last three densities equation (7) and (16)

age(year)	2965 stems/hm ²		4304 stems/hm ²		6726 stems/hm ²	
	(7)	(16)	(7)	(16)	(7)	(16)
2.0	73.26	73.30	64.29	64.30	64.32	64.33
3.0	100.18	100.20	86.33	86.33	84.26	84.26
4.0	116.51	116.52	99.76	99.76	96.40	96.40
5.0	128.93	128.94	110.10	110.10	105.88	105.88
6.0	139.23	139.24	118.80	118.81	113.99	114.00
7.0	148.16	148.17	126.48	126.48	121.29	121.29
8.0	156.15	156.16	133.45	133.45	128.05	128.05
9.0	163.42	163.43	139.91	139.91	134.45	134.45
10.0	170.15	170.16	145.99	145.99	140.60	140.60
11.0	176.44	176.45	151.77	151.78	146.57	146.58
12.0	182.37	182.38	157.33	157.33	152.43	152.43
13.0	188.01	188.01	162.69	162.69	158.21	158.21
14.0	193.39	193.39	169.91	167.91	163.94	163.94
15.0	198.55	198.56	173.01	173.01	169.66	169.66
16.0	203.53	203.54	178.01	178.01	175.38	175.38
17.0	208.35	208.35	182.93	182.93	181.13	181.13
18.0	213.02	213.03	187.79	187.79	186.92	186.92
19.0	217.57	217.58	192.61	192.61	192.76	192.76
20.0	222.01	222.01	197.38	197.38	198.66	198.66

and $\kappa > 0$. Equation (2) does not describe such data very well, the right choice for these stand should be (7). Taking the density of 6726 stems/hm² as an example, by the relation between the parameters, the Chapman-Richards function should be:

$$Y(t) = 127.5245 (0.85297 e^{0.1076t} - 1)^{\frac{1}{1-4.1654}}$$

This model has t_0 and an inflection point, but no asymptote. From (8) and (9), it is known that $t_0=1.48$ and $t_1=14.74$, these results coincide with that from the Schnute model.

Table 3 contains the values for parameter A , B , κ , and m for the three densities, these values are calculated from y_1 , y_2 , a , and b for the same densities. With such estimated parameters, (7), the second exceptional case of the Chapman-Richards function, is used to predict the diameter for the three densities along with (16) or the Schnute model, the predicted values are listed in Table 4, showing the two produced identical results.

In summary, the Chapman-Richards function will fit the last three densities, and the fitted results should be identical to those from the Schnute model. Equation (5) and (7), two exceptional cases of Chapman-Richards function, are capable of tracking the growth after the mortality induced by competition.

Conclusions

The Schnute model with $a \neq 0$ and $b \neq 0$ may be regarded as an existing model since its assumption, the form of solutions, and the cross-over and inflection points with which determine the curve shape are identical to those for the Chapman-Richards function. In fact, the Schnute model is one of the solutions to (1) if the latter is used to model a growth process with two known stages.

Compared with the Schnute model, the Chapman-Richards function is simple and convenient in both formulation and its cross-over and inflection point functions. The parameters in Chapman-Richards function also have a clear biological interpretation.

When parameters in (1) are unconstrained, the Chapman-Richards function can also be very versatile. Any data set which can be fitted by the Schnute model

should also successfully fitted by the Chapman-Richards function.

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Appendices

(A) The general solution to the Chapman-Richards function

The differential equation is

$$\frac{dy}{dt} = \eta y^m - \kappa y \quad (A1)$$

Multiply both sides of (A1) by $(1-m)y^{1-m}$, it becomes:

$$(1-m)y^{1-m} \frac{dy}{dt} = (1-m)(\eta - \kappa y^{1-m}) \quad (A2)$$

Let $x = y^{1-m}$, then there is

$$\frac{dy}{dt} = (1-m)y^{1-m} \frac{dx}{dt}$$

Substitute the above (A2) gives:

$$\frac{dy}{dt} = (1-m)(\eta - \kappa x) \text{ or } \frac{dx}{\eta - \kappa x} = (1-m)dt \quad (A3)$$

The solution to (A3) is

$$\ln(\eta - \kappa x) = -\kappa(1-m)t + c \quad (A4)$$

where c is intergration constant

Placing $x = y^{1-m}$ into (A4), the general solution is:

$$y = \left(\frac{\eta}{\kappa} - \frac{c_3}{\kappa} e^{-\kappa(1-m)t} \right)^{\frac{1}{1-m}}, c_3 = e^c \quad (A5)$$

Let $\alpha = \frac{\eta}{\kappa}$, $\beta = -\frac{c_3}{\kappa}$, $\gamma = \kappa(1-m)$, $\delta = 1 - \frac{1}{1-m}$, can

be simplified as: $y = (\alpha + \beta e^{\gamma t})^{\delta}$

(B) The General solution to the Schnute model

The differential equation is:

$$\frac{1}{Z} \frac{dZ}{dt} = -(a + bZ) \quad (B1)$$

The general solution to (B1) is:

$$\frac{Z}{a + bZ} = e^{-at - bt}, e^t \text{ is integration constant} \quad (B2)$$

Since $Z = \frac{1}{y} \frac{dy}{dt}$, (B2) can be written as:

$$Z = \frac{1}{y} \frac{dy}{dt} = \frac{ac_1 e^{-at}}{1 - bc_1 e^{-at}} + c_1 = e^t \quad (B3)$$

(B3) can be integrated as:

$$\ln(y) = \frac{1}{b} \ln(1 - bc_1 e^{-at}) + c'' \quad (B4)$$

where c'' is integration constant.

The general solution to (B1) is:

$$y = c_2 (1 - bc_1 e^{-at})^{\frac{1}{b}}, c_2 = e^{c''} \quad (B5)$$

Let $\alpha = c_2^{\frac{1}{b}}$, $\beta = -bc_1 c_2^{\frac{1}{b}}$, $\gamma = -a$, $\delta = 1/b$, (B5) can also be simplified as $y = (\alpha + \beta e^{\gamma t})^{\delta}$